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The effects of animal feeding activities on element release from deciduous forest litter and soil organic matter

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Summary :

Soil fauna are implicated as important regulators of nutrient flux pathways but their roles have yet to be quantified under field conditions because of a lack of basic information on the processes involved. We review experiments which demonstrate some of the variables influencing animal-mediated fluxes of mineral elements from leaf litter and soil organic matter : the groups of fauna, grazing intensity, temperature and the nature of the resources.

Enchytraeids, Collembola, millipedes and lumbricid worms were found to enhance sodium, potassium, calcium and mineral nitrogen losses from oak leaf litter. The effects of animal grazing were largest for ammonium-N and losses of nitrogen in this form were significantly correlated with the fresh weight of animals in the treatments. Enchytraeids had little effect on nitrogen release while *Lumbricus rubellus* produced ammonium-N fluxes nearly 60 times control levels; the arthropod groups having intermediate effects. However this relationship is complicated by non-linear effects of grazing intensity and is also manifested through the nutrient content of the resources the animals are exploiting.

Patterns of nutrient losses from L, F and H-layer materials from oak woodlands illustrate this last effect but also show that the animals amplify existing patterns of mineral element fluxes including nitrogen as nitrate. Temperature is an important variable determining the magnitude of the response for a given resource type, particularly for ammonium-N. Nitrogen losses from leaf litter as ammonium were 5 to 7 times higher at 15-20° C than at 5° C. Abiotic processes, particularly wetting and drying, may also be important at high temperatures under field conditions.

Further attempts towards quantifying these processes under field conditions were initiated by experiments which show that the fauna can mediate in nitrogen fluxes between freshly fallen leaf litter and the root/mycorrhizal system of beech trees. Thus the fauna effectively disrupt the normal timecourse of nitrogen mineralisation by microorganisms.

Key words : interactions, nutrients, nitrogen, mineralization, woodlands.

I. Introduction

There is an extensive ecological literature suggesting that soil animals have important roles in nutrient cycles, but the evidence is semi-quantitative, circumstantial or indirectly derived from nutrient budgets. Numerous studies could be cited, many from previous symposia in this series, demonstrating the roles of animals in enhancing nutrient mobilisation and mineralisation (see review by ANDERSON, COLEMAN & COLE, 1981), and yet these processes have not been quantified in any natural system.

The two principal reasons for the intractability of the problem appear to be that, firstly, the natural field systems, particularly woodlands, are too complicated to manipulate or monitor at the microsite scale at which these processes operate. Secondly, the effects of animals on nutrient fluxes may not be simply quantified in terms of energy or nutrient transfers. Evidence of complicated interactive effects can be seen in the effects of animals on microbial activity through grazing on fungi and bacteria (COLEMAN *et al.*, 1978; BÅÅTH *et al.*, 1978; HANLON & ANDERSON, 1979), litter comminution (HANLON & ANDERSON, 1980; HANLON, 1981a,b) and the influence of gut passage on bacterial biomass and viability (ANDERSON & BIGNELL, 1980; ANDERSON & INESON, 1983).

One approach to investigating these interactions has been through the use of complex laboratory systems, or microcosms, which PATTEN & WITKAMP (1967) used to demonstrate that snails and millipedes were integral to the transfers of ^{137}Cs from litter to plant seedlings. Further experiments by WITKAMP & FRANK (1969, 1970) investigated some of the variables affecting the enhancement of potassium and magnesium mobilisation through the feeding activities of millipedes and it was concluded that the mechanism involved in the effect was the reduction of microbial immobilisation of nutrients. Analyses were not made for nitrogen or phosphorous in these experiments, although these elements are characteristically immobilised by the microorganisms involved in litter decay.

More recently a number of workers have demonstrated the potential of protozoa and nematodes grazing on fungi and bacteria for increasing nitrogen and phosphorous mineralisation and turnover rates (COLE *et al.*, 1978; ANDERSON *et al.*, 1981; BÅÅTH *et al.*, 1978 and CLARHOLM *et al.*, 1981). Comparatively little work has been carried out on the meso and macrofauna particularly in deciduous forests. INESON, LEONARD & ANDERSON (1983) found that Collembola enhanced nitrogen mineralisation and cation leaching from leaf litter during the early stages of decomposition, though VISSER, WHITTAKER & PARKINSON (1981) found no evidence of these effects in shorter term experiments.

The potential effect of the mesofauna, however, appears small in relation to the large nutrient fluxes, particularly, of ammonium-N, induced by litter-feeding millipedes (Diplopoda) and woodlice (Isopoda) (ANDERSON & INESON, 1983). We review here a series of experiments which quantify some of the variables involved in these effects : the groups of fauna; grazing intensity ; temperature and nature of resources utilised by the animals. The effect of these variables are measured as nitrogen, calcium, potassium and sodium fluxes. This sequence of elements theoretically represents a gradient from the biotic mineralization of N to the predominantly abiotic leaching processes mobilising sodium.

Our objectives are to formulate a model quantifying the role of soil animals, particularly macroarthropods, in nutrient cycling in deciduous woodlands. We recognise the problems of relating laboratory experiments to natural conditions and our intention is to develop new hypotheses which are testable in the field.

All the current series of experiments were carried out using the microcosm chambers described by ANDERSON & INESON (1982) which facilitate measurements of gaseous and leachate losses from soil and litter materials induced by animal feeding activities. Details of the preparation of materials and analyses are given in ANDERSON, INESON & HUISH (1983).

II. Faunal groups

Our intention is to investigate the extent to which nutrient fluxes mediated by soil animals can be attributed to macro- and meso- fauna and to indirectly assess the contribution of microfauna to this process.

The effects of a range of animal groups on nutrient mobilisation from forest litter were investigated by ANDERSON, INESON & HUISH (1983) and the results are summarised in Table I. Numbers of animals in individual treatments were chosen to fall within the upper range of densities found in aggregated field populations in the acid deciduous forest soils under investigation. The results show that, in general, the animal treatments result in enhanced losses of all elements over controls but individual effects for animals and groups are not statistically significant in many cases. Animals had the most marked effects on ammonium fluxes with increased leachate concentrations of 10-20 times control levels for the millipedes and more than 60 times control for earthworms. The effects of the Collembola and enchytraeids are comparatively

TABLE I

Effect of animal grazing upon the release of elements from F layer materials. Results expressed in mg/g dry weight of litter over a 6 week period. Significance levels : * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ for treatments when compared to no animals, n = 3.

	Control (without animals)	Enchytraeids	*Lumbricus rubellus*	*Tomocerus minor*	*Orchesella villosa*	*Polydesmus angustus*	*Iulus scandinavius*	*Glomeris marginata*
NH_4-N	0.03	0.02	1.78***	0.10*	0.10*	0.38*	0.68***	0.54**
NO_3N	0.002	0.002	0.021***	0.004	0.004	0.006	0.008*	0.003
Na^+	0.14	0.14	0.28***	0.17*	0.19***	0.22*	0.18*	0.15
K^+	0.13	0.13	0.46***	0.20	0.17	0.29	0.44	0.38***
Ca^{++}	0.93	0.75**	1.88***	0.84	0.81*	0.93	0.97	1.01
mean leachate pH	5.3	5.4	5.6	5.3	5.3	5.4	5.5	5.2
wet weight of animals (g)	-	0.03	1.00	0.04	0.04	0.14	0.49	0.59
number of animals	-	25	3	15	15	3	4	4

small since the treatments contained much lower biomass of these animals. However, there is an overall correlation between increased ammonium-N mobilisation and faunal biomass ($r^2 = 0.95$, $P < 0.001$) which allows the calculation of equivalent ammonium-N release per gram of animal. Expressed on this basis the Collembola have a larger effect of nitrogen losses (2.5 mg.g litter^{-1} . animal^{-1}) than other groups, with the exception of *Polydesmus angustus* (2.7 mg.g litter^{-1} . g animal^{-1}). Such a relationship may provide a basis for extrapolating laboratory results into estimates of community involvement in nutrient fluxes in the field, but ANDERSON *et al.* (1983) have shown that nutrient release from leaf litter by animals is not necessarily a function of grazing intensity. Treatments with 2, 4, 6 & 8 *Glomeris marginata* showed significant increases in nutrient release over control levels but maximum effects for N mobilisation were induced by 4 animals, 6 and 8 animals producing a proportionally smaller response (Fig. 1). Similar experiments with the woodlouse (*Oniscus asellus)* however showed that there was a linear relationship between number of animals and element concentrations in leachates. A direct comparison between the effects of *G. marginata* and *O. asellus* nutrient release are not possible because *O. asellus* has poor long-term survival in microcosms beyond 6 weeks, particularly at high densities, whereas the maximum effects of *G. marginata* on N release are not manifested until after this period.

Experiments which use the macroarthropod number as a variable may be considered analogous to the range of densities found in aggregated populations in the field. The reproductive recruitment to these populations is long term and the effect of these population changes will not normally affect local aggregations of individuals. The macroarthropod grazing effects may be therefore seen as a temporal perturbation, of variable duration, before the animals move on or the aggregation disperses. The effects of removing animals have been studied and reveal that animal induced mobilisation of N, for example, may continue for several weeks after removal (ANDERSON & INESON, 1983).

Microarthropods, such as Collembola, have a comparatively short generation time and numbers of animals in treatments can increase considerably during the time course of several months used in some of the microcosm experiments. Collembola grazing has small effects on nutrient release but there is a transfer of N to the Collembola biomass, which has a much more rapid turnover than that of the macroarthropods (INESON, LEONARD & ANDERSON, 1983). This is a continuation of an effect seen for protozoa and nematodes grazing, where short generation times means that animal populations may track food supply. Such relationships may be complicated by spatial heterogenity of the environment (ELLIOT *et al.*, 1980; ANDERSON & INESON, 1983) which may also serve to stabilise interactions.

III. Temperature effects

WITKAMP & FRANK (1970) and CLARHOLM *et al.* (1981) have demonstrated, for cations and mineral nitrogen respectively, that temperature is a major determinant

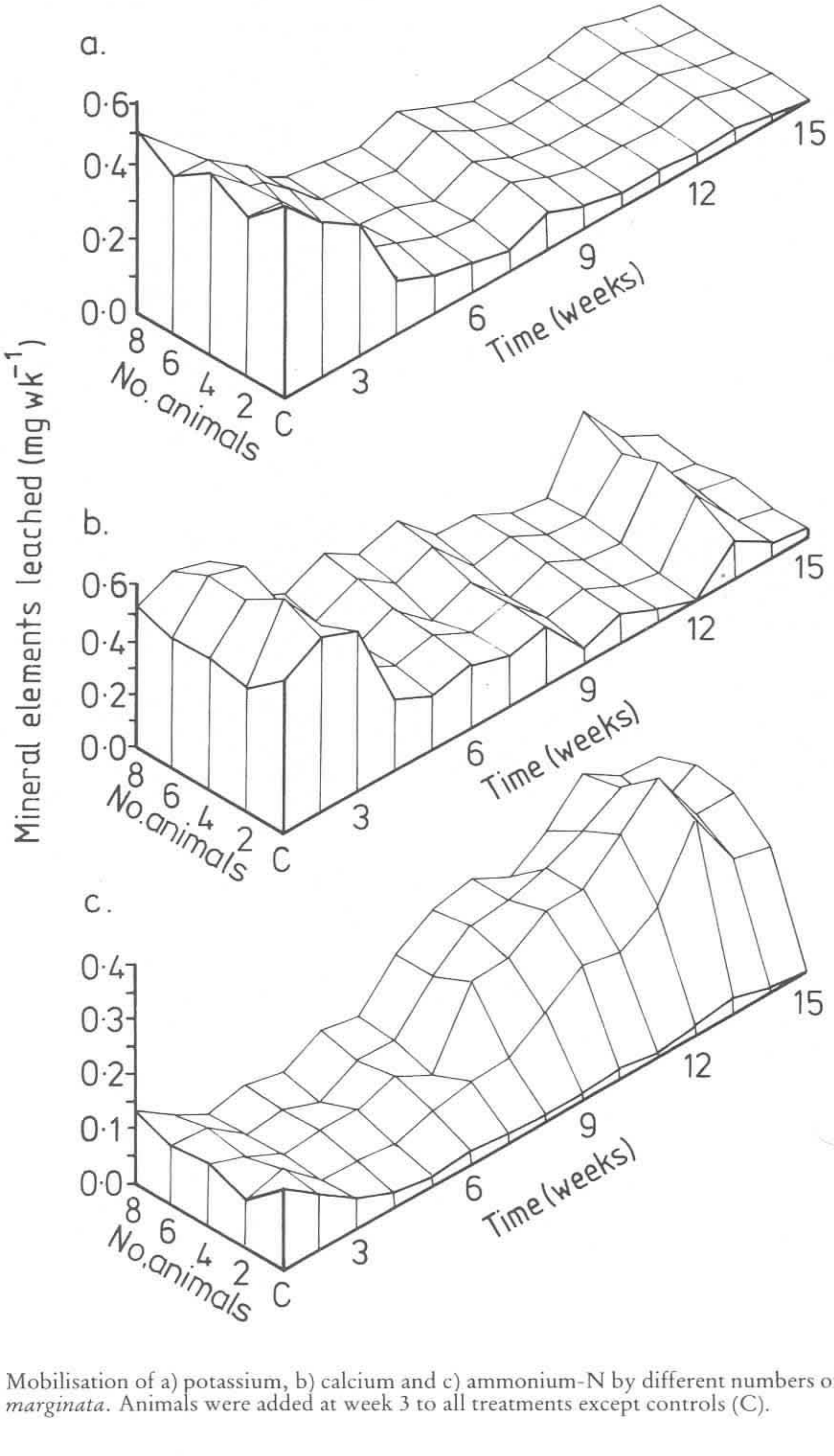

Figure 1 Mobilisation of a) potassium, b) calcium and c) ammonium-N by different numbers of *Glomeris marginata*. Animals were added at week 3 to all treatments except controls (C).

of nutrient mobilisation in forest soils. WITKAMP & FRANK (1970) concluded that leaching of potassium and magnesium from leaf-litter was primarily affected by temperature and only secondarily by millipede grazing, while the experiments of CLARHOLM *et al.* (1981) do not differentiate between animal, microbial or abiotic processes. Our results (Table II) are not directly comparable to these studies but support their conclusions in part. Analysis of variance for temperature effects on mineral element leaching from ungrazed controls showed no significant relationships for mineral nitrogen or sodium but significant effects for potassium ($P < 0.05$) and calcium ($P < 0.05$). Paired t-tests for individual treatments showed that these effects were located in significant differences between potassium losses at 10, 15 and 20° C and significantly higher calcium losses at 20° C than at 10° or 5° C. Thus leaching of potassium is 44 % higher, and calcium 60 % higher, at 20° C than 5° C.

Millipedes were found to have no significant effect on potassium and calcium leaching in most treatments and although sodium losses were enhanced to a maximum of 2.6 times control level at 20° C there was no clear temperature related response. In all cases, however, enhanced leaching of simple cations are small in relation to the large fluxes of ammonium-N induced by the animals at 15-20° C. Increases in nitrate-N at these temperatures were small but significant and we attribute this to enhanced nitrification under these warm, moist conditions. The fluxes of ammonium-N show no conventional temperature response since leachate concentrations more than double for a 10° C rise in temperature from 10 to 20° C and show a tenfold increase from 5 to 15° C. CLARHOLM *et al.* (1981) recorded an enhancement of N mineralisation of approximately 50 times between 5° C and 20° C in pine forest soil material incubated at high moisture levels.

WITKAMP & FRANK (1970) concluded that mineral element release effected by animal feeding activities would be expected to follow a $Q_{10} = 2$ relationship, but that this would be an exception under field conditions because of interactions between temperature and moisture. They observed that high temperatures and low moisture inhibited microbial and millipede activities. Upon rewetting, millipedes continued feeding at the same rates as before drying but there was a characteristic flush of microbial activity and element release followed by immobilisation during the subsequent phase of microbial growth. Nutrient mobilisation through these wetting and drying cycles has been shown in the laboratory to be more significant than biotic processes at high temperatures (WITKAMP & BARZANSKY, 1968; WITKAMP, 1969) but their significance for nutrient fluxes from litter in the field remains to be determined.

In the present series of experiments, and those of CLARHOLM *et al.* (1981), moisture was controlled in the experimental material. Even so, temperature effects on simple cations showed less than a $Q_{10} = 2$ relationship but a far larger response for nitrogen mineralisation. This suggests that the effects of animals on nutrient fluxes are not simply related to excretion in the case of nitrogen mineralisation as suggested by

TABLE II

The effect of *Glomeris* on mineral element release from oak leaves at a range of temperature. Value given, in μg per g dry weight of litter, are cumulative means of three replicates (± 1 S.E.) over a period of nine weeks. Asterisks indicate where animal treatments and controls at the same temperature are significantly different ($P \leq 0.05$). Animal treatments are also shown as a proportion of controls.

Temperature (°C)	5°			10°		
No. animals	0	4	Ratio 4/0	0	4	Ratio 4/0
Ammonium-N	21.2 (± 1.6)	19.4 (± 3.7)	0.9	16.7 (± 1.4)	36.9 (± 9.3)*	2.2
Nitrate-N	5.6 (± 1.8)	5.2 (± 1.7)	0.9	4.4 (± 1.5)	4.1 (± 0.9)	0.9
Sodium	32.9 (± 3.2)	44.8 (± 6.4)	1.4	30.7 (± 4.7)	51.2 (± 7.8)*	1.7
Potassium	57.7 (± 3.6)	63.3 (± 16.9)	1.1	42.9 (± 3.3)	75.4 (± 9.1)*	1.8
Calcium	334.4 (± 53.4)	431.0 (± 51.9)	1.3	373.5 (± 12.8)	380.1 (± 14.4)	1.0
Temperature (°C)	15°			20°		
No. animals	0	4	Ratio 4/0	0	4	Ratio 4/0
Ammonium-N	12.2 (± 2.4)	130.4 (± 56.6)*	10.7	15.7 (± 3.5)	98.4 (± 24.7)*	6.3
Nitrate-N	2.2 (± 0.4)	6.0 (± 2.1)*	2.7	2.9 (± 0.4)	10.1 (± 3.2)*	3.5
Sodium	33.4 (± 3.2)	51.7 (± 5.0)*	1.6	25.9 (± 1.0)	66.8 (± 13.6)*	2.6
Potassium	81.6 (± 11.5)	101.4 (± 10.9)	1.2	82.9 (± 12.0)	81.1 (± 3.3)	1.0
Calcium	489.5 (± 70.2)	563.4 (± 66.6)	1.2	534.8 (± 20.7)	817.1 (± 37.3)*	1.5

ANDERSON, COLEMAN & COLE (1981), and that the element concentrations of the resources exploited by the animals may primarily determine the magnitude of the fluxes. This process is demonstrated by the effects of millipedes on nutrient leaching from a range of forest floor materials.

IV. Resource types

Nitrogen and cation losses from the litter layer (L), fermentation layer (F) and humus layer (H) materials from a mature oak-woodland (Stoke Woods) are shown in Table III. Losses of sodium, potassium and calcium were increased by Millipede grazing in all cases but the effects, as in the previous experiments, are small in comparison with N mobilisation.

TABLE III

Effects of *Glomeris marginata* grazing on element release from different organic soil layers. Results in mg/g d.wt. over a 9 week period.

	L layer		F layer		H layer		H layer	
	Stoke Woods		Stoke Woods		Stoke Woods		Perridge	
Number of animals	0	4	0	4	0	4	0	4
Ammonium-N	0.01	0.13	0.52	1.46	0.02	0.24	0.16	0.34
Nitrate-N	0.00	0.01	0.39	1.16	0.12	0.68	0.02	0.01
Sodium	0.03	0.52	0.04	0.11	0.02	0.05	0.07	0.06
Potassium	0.08	0.10	0.12	0.54	0.06	0.16	0.11	0.21
Calcium	0.44	1.22	0.47	1.18	0.29	0.72	0.07	0.06
Leachate pH	4.6	4.7	5.4	5.2	4.5	4.2	4.6	4.9

Leachate from L-layer material contained small concentrations of nitrate-N and the ammonium-N flux showed the expected enhancement by animals. Leachates from the F-layer material, however, have similar concentrations of nitrate-N and ammonium-N and both forms of mineral N were increased by approximately three times control levels by the animals. Nitrate-N concentrations in Stoke Woods H-layer material were higher than those of ammonium-N and although the animals produced a proportionately greater enhancement of ammonium than nitrate, nitrate remained the predominant form of mineral nitrogen. The enhancement of nitrate-N fluxes was unexpected and the same series of experiments were carried out with H-layer material from a second-woodland (Perridge) to investigate this effect. The results showed the opposite pattern with ammonium-N, the dominant form of mineral N. Thus the effect of *Glomeris* was to amplify existing patterns of mineral N fluxes in H-layer material :

ammonium-N by twelve times and nitrate-N seven times in the Stoke Woods material, while the Perridge material showed a doubling of ammonium-N fluxes but little change, or a small decrease, for nitrate-N.

V. Processes of nutrient mobilisation

Decomposition and nutrient losses from litter and soil organic matter involve three distinct processes, defined by SWIFT, HEAL & ANDERSON (1979) as catabolism (enzyme mediated processes which ultimately result in mineralisation), comminution (the physical destruction of the resource by biotic or abiotic processes) and leaching (the removal of soluble materials by water). The relative importance of these processes for fluxes of different elements relates directly to their availability and requirement by saprotrophs (fungi, bacteria and animals) involved in organic matter decomposition.

Sodium and potassium are generally present in excess of saprotroph requirements and are leached rapidly from decomposing materials until the concentrations approach those of microbial tissues (GOSZ, LIKENS & BORMANN, 1973; CROMACK *et al.*, 1977). WITKAMP & BARZANSKY (1968) have shown significantly higher potassium retention by microbially inoculated leaves than in leached sterile controls but these microbial pools are insignificantly small in relation to the total fluxes. Potassium and sodium are predominantly present in ionic form in plant tissues and therefore the fluxes of these elements may be largely independent of biologically mediated mineralisation processes. It is not therefore unexpected that the effect of animals on losses of potassium and sodium from leaf litter are small and do not show a consistent temperature related response.

Calcium is mainly biologically bound in primary cell walls as calcium pectate and its mobilisation is therefore effected by catabolic processes and comminution. Losses of calcium from leaf litter tend to follow the time course of carbon mineralisation and are significantly affected by animal feeding activities (ANDERSON & INESON, 1983). However, since calcium mineralisation shows less than a $Q_{10} = 2$ relationship without animals and no clear temperature response by microflora and fauna, microbial immobilisation as demonstrated by CROMACK *et al.* (1977), may be involved.

Nitrogen is limiting to saprotroph populations in most terrestrial ecosystems and is immobilised in microbial tissues during the early stages of decomposition. The mineralisation of this nitrogen pool is not generally thought to occur until growth of the microbial population becomes carbon limited and the carbon/nitrogen ration of the resource approaches that of microbial tissues. Losses of mineral nitrogen from litter layer material, in the absence of animals, were not enhanced at high temperatures because immobilisation through microbial growth increases to a greater extent than mineralisation.

The effects of animals on nitrogen mineralisation is not simply to disrupt this pattern of microbial immobilisation but also to amplify the existing fluxes in soil organic matter as well as litter. This effect was particularly marked in the humus layers where grazing increased the amount of nitrogen mineralised as nitrate. It is generally assumed that acid soils have an ammonium based economy (BARTHOLOMEW & CLARK, 1966; ALEXANDER, 1977) because nitrifying bacteria have pH optima higher than ambient conditions, yet the H-layer controls from the two sites show different forms of mineral nitrogen fluxes under comparable pH conditions, litter types and parent soils. The effects of animals in amplifying these fluxes can be related to the reduction of fungal biomass through comminution and a shift in microbial activity towards bacterial dominance (HANLON & ANDERSON, 1979, 1980). Ammonium may largely be derived from lysed fungal hyphae through the activities of ammonifying bacteria in the animal guts (ANDERSON & INESON, 1983) while nitrate may be either derived heterotrophically from grazed fungi or from autotrophic nitrification stimulated by increased ammonium availability. The processes of enhancement are not simply excretion. Experiments with ^{15}N labelled Millipedes showed that only approximately 7 % of the mobilised nitrogen was attributable to the animals (ANDERSON & INESON, unpublished data).

VI. Conclusion

The experiments reported here demonstrate that nitrogen mineralisation, and to a smaller extent fluxes of potassium, sodium and calcium, are significantly affected by most groups of saprotrophic invertebrates. These effects, to a large extent, transcend taxonomic identity and may be related to the biomass or activity of functional groups of animals (macrofauna, mesofauna and microfauna) acting on resources of known nutrient content. However, the non-linear effects of *Glomeris* grazing emphasise that the relationship is not a direct one and is expressed through synergistic and antagonistic interactions with the soil and litter flora. Thus further experimental work is required particularly under field conditions, before it is possible to attempt a synthesis of the role of soil fauna in nutrient cycling. The potential importance of this role is, however, indicated by experiments where attached roots and mycorrhizae of beech trees (*Fagus sylvatica* L.) were introduced through ports in the sides of experimental chambers. Ammonium release in treatments without roots was 51 % higher with millipedes than controls, but 48 % of the mobilised ammonium was taken up by the root/mycorrhizal complex. Thus animals can mediate in nitrogn transfers from leaf litter to roots and short-circuit the time course of microbially dominated nitrogen mineralisation processes.

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Discussion

SWIFT, M.J. (1) : Could you comment on the possible mechanisms involved in the transformation of organic-N to ammonium and nitrate in view of your suggestion that excretion is only a very small component of this pathway ?

(2) : Traditional microbiological theory would suggest that in the presence of high C and energy, mineral forms of N will be immobilized by the microflora. Could you tell us what the C/N ratio of the litter in your experiments was at the times of major N release and speculate on which immobilization is low ?

(3) : Might one of the reasons for low immobilization be the inaccessibility of carbon and energy ? The shift from a fungal-dominated to a largely bacterial flora following grazing could mean that the microflora is unable to process the remaining plant polymers and thus has only a low N demand.

ANDERSON, J.M. : (1) : At the present time we are unable to account for the nitrate by either heterotrophic or autotrophic nitrification. Ammonnifying bacteria are a dominant component of the faecal flora and may be acting on the ingested fungal protoplasm, but we do not get similar increases in nitrifiers.

(2) : The C/N ratio of the litter (including the microflora) is about 100/1 and even the humus layers have higher C/N ratios than those at which mineralization theoritically occurs.

(3) : I agree and the effect is enhanced by the composition of organic matter in faeces and organic matter in soil.

COLEMAN, D.C. : I would like to second Dr. ANDERSON's comment on the effect of animal grazers on microbes affecting the quality of the returned nitrogenous material. There can be significant amounts of aminonitrogen returned to the soil solution by bacterial-feeding nematodes under conditions of luxury consumption (as measured under laboratory conditions).

ANDERSON, J.M. : Yes, your group has shown this very elegantly.

LEE, K.E. : New Zealand work indicates that mycorrhizal fungi inhibit decomposition processes in pine litter. Might this have some significance in your experiments, where mycorrhizal fungi are present, whether animals are present or not ?

ANDERSON, J.M. : We have some evidence of interactions between mycorrhizal fungi and litter Basidiomycetes, and are investigating these phenomena.

GHILAROV, M. : Are the mycorrhizae taking up the nitrogen mineralized by the animals ?

ANDERSON, J.M. : Yes, but it is interesting that the uptake of ammonium by mycorrhizae is proportionately larger in treatments with animals than controls with mycorrhizae but no animals. It may be that other animal related effects, such as phosphorus mobilization, are involved.

EIJSACKERS, H. : Did you notice any effect of moulting on the grazing activity of the macroarthropods resulting in a cyclic release of nutrients ?

ANDERSON, J.M. : We have followed the relationship between fungal and collembolan populations in relation to nutrient release but not for macroarthropods. In the laboratory we control for size and moult status, where possible, in order to simulate grazing effects at different densities within aggregated populations rather than effects in time. Eventually the long term pattern of nutrient release from macroarthropod tissues will have to be investigated for a full understanding of these processes.

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